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TWO NEW GENERA IN THE NEOTROPICAL RIODINID TRIBE NYMPHIDIINI (RIODINIDAE)

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ABSTRACT. Two new monotypic Neotropical riodinid genera, *Behemothia*, new genus, and *Protonymphidia*, new genus, are described in the myrmecophilous tribe Nymphidiini, to respectively contain the taxa *godmanii* Dewitz, 1877, formerly treated in *Pandemos* Hübner, [1819], and *senta* (Hewitson, 1853), formerly treated in *Adelotypa* Warren, 1895. These genera are characterized and their systematic position discussed.

Additional key words: cladistics, morphology, Theopeiti.

The butterfly family Riodinidae is almost entirely confined to the Neotropics, where approximately 1300 species or 95 percent of the familial diversity occurs (Heppner 1991). Despite constituting a significant proportion of the Neotropical butterfly fauna in low and middle elevation forest habitats (Robbins 1982, 1993), and containing numerous genera that exhibit fascinating adult and early stage biology (Callaghan 1983, DeVries 1990, 1991, 1997, Hall 1999b), the Riodinidae has received relatively little systematic attention, and the first cladistically derived phylogenies for the group were only very recently generated (Hall 1998, 1999a, Penz & DeVries 1999).

This paper forms part of a broader study to create a natural generic classification for the largest and probably systematically least well understood of the riodinid tribes, the Nymphidiini Bates, 1859 (*sensu* Hall 1999a [=Lemoniini + Nymphidiini of Harvey 1987]) (Harvey 1987, Hall 1999a, b). A recent comprehensive cladistic analysis of the nymphidiine subtribe Theopeiti (*sensu* Hall 1999a), based on the inclusion of all known species (75) and over 100 characters of male and female morphology and wing pattern, indicated the existence of five monophyletic clades worthy of generic status (Hall 1999a, b) (see Fig. 1), however only the single generic name *Theope* Doubleday, 1847, was available for them. One genus, *Archaeonympha* Hall, 1998, has subsequently been described (Hall & Har-

vey 1998), another is soon to be described (Hall & Harvey in prep.), and the remaining two are described here to contain the taxa *godmanii* Dewitz, 1877, and *senta* Hewitson, 1853, currently treated in the genera *Pandemos* Hübner, [1819], and *Adelotypa* Warren, 1895, respectively (Bridges 1994). The terminology for male and female genital and abdominal structures follows Klots (1956) and Eliot (1973), while nomenclature for venation follows Comstock and Needham (1918).

Behemothia Hall, new genus

Figs. 2A–D; 4A–F; 6A–D

Type species. *Behemothia godmanii* (Dewitz 1877)

Description. MALE: typical forewing length 32–33 mm. *Wing shape:* forewing costa smoothly convex, distal margin rounded, apex markedly falcate; hindwing rounded and slightly elongate. *Venation* (Fig. 4A): four forewing radial veins. *Dorsal surface:* forewing ground color russet-brown, dark brown mark at discal cell end; a narrow postdiscal white band curves from costa to vein Cu2 then becomes lilac as far as anal margin, basal half of wing lilac except for costal, basal and discal russet-brown areas; distal fringe black. Hindwing entirely blue except for russet-brown anal margin and small area of black scaling at base of costal margin; fringe black. *Ventral surface:* forewing ground color brown; white postdiscal band as on dorsal surface but broader and entirely white; basal area of wing black except for brown at costal margin and very base of wing in cell Cu2, and blue in basal half of discal cell and upper portion of cell Cu2; a black spot discernible at proximal edge of basal black in cell Cu2, typically with some lilac scaling distally, another smaller one within brown scaling further towards wing base and a variably prominent one within blue scaling of discal cell. Hindwing ground color brown; dark brown line marks discal cell end, a dark brown

spot towards base of cell Sc+R1 above discal cell; a dark brown post-discal band extends from costa to vein Cu2 then curves inwards in cell Cu2, band displaced proximally in cell Sc+R1 and enlarged into large square surrounded by whitish scaling. *Head*: ventral surface of labial palpi a mixture of pale and dark brown scaling on segments one and two, pale brown on very short third segment, dorsal surface entirely dark brown (Fig. 4B). Eyes bare and brown (in dried specimens), pale brown scaling at margins. Frons dark brown, paler brown at margins and ventrally. Antennae brown with whitish scaling at base of each segment becoming more prominent towards clubs dorsally, narrow nudum region devoid of scaling along inner edge of shaft; flattened clubs brown dorsally and orange-brown ventrally. *Body*: dorsal surface of thorax and abdomen, including patagia, russet-brown, ventral surface pale gray-brown. All legs pale gray-brown; tarsus of foreleg unimerous and elongate, coxa elongate (Fig. 4D); midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tarsal segments one to four, numerous further spines along entire inner distal margin of first tarsal segment (Fig. 4F). *Genitalia* (Fig. 6A, B): uncus more elongate dorsally, separated from triangular tegumen by triangular lateral fenestration; falcis of average size and shape; vinculum broad, especially ventrally, and incomplete dorsally (i.e., not extending around entire anterior margin of tegumen) where it is folded over; valvae rectangular with a prominent angular dorsal projection and a smaller ventral one; aedeagus gradually tapers to a very narrow and slightly undulating tip with a ventral bulge before tip, a single large cornutus is teardrop-shaped in lateral view and crescent-shaped in dorsal view; pedicel short, heavily sclerotized, and broad, especially ventrally. Last tergite a plain rectangle; last sternite rounded anteriorly, produced into two triangular points posteriorly, distal third heavily sclerotized and dorsally invaginated (Fig. 6C).

FEMALE: differs from male in following ways: *Dorsal surface*: white postdiscal forewing band broader at costa, lilac present on forewing only in tomus as extension of white postdiscal band; fringe dark brown. Hindwing entirely russet-brown except for dark brown scaling at base of costal margin, marking cell end and forming a faint postdiscal band; fringe dark brown. *Ventral surface*: blue scaling at base of forewing absent, basal half of wing a paler dark brown, highlighting two basal dark brown spots in cell Cu2 and three spots in discal cell, one marking cell end, and a postdiscal line of dark brown spots proximal to postdiscal white band. Hindwing an even plain brown color, typically with slightly fainter dark brown markings. *Head*: second palpal segment slightly more elongate (Fig. 4C), ventral surface of third segment a mixture of dark and pale brown scaling. White scaling at base of antennal segments reduced, especially on dorsal surface, considerably broader nudum region along inner edge of shaft. *Body*: foreleg with one or two spines at inner distal tip of tarsal segments one to four (Fig. 4E). *Genitalia* (Figs. 6D): corpus bursae narrow and elongate, signae triangular, tooth-shaped sclerotized invaginations with jagged basal margin; ductus bursae and ductus seminalis unsclerotized; ostium bursae consists of a broad sclerotized band ventrally which narrows laterally and dorsally.

Diagnosis. The single species of *Behemothia*, *B. godmanii*, bears little resemblance to any other riodinid. The combination of its large size, markedly falcate forewing apex, black scaling at the base of the dorsal hindwing and ventral forewing, and russet-brown dorsal ground color covered with lilac and blue scaling in the male is unique.

Etymology. The name is derived from the Hebrew word "behemoth", meaning "enormous animal," in reference to the huge size of this species, one of the largest in the Riodinidae.

Systematic position: The genus *Pandemos* was erected by Hübner ([1819]) to include the single new species *arcassa* (a synonym of *pasiphae* Cramer 1775), and Hewitson (1870) and Dewitz (1877) subsequently added *palaeste* and *godmanii* respectively (Stichel 1930–31, Bridges 1988, 1994). However, the only unifying characteristic of these three species is their huge size, and Harvey (1987), D'Abrera (1994) and DeVries

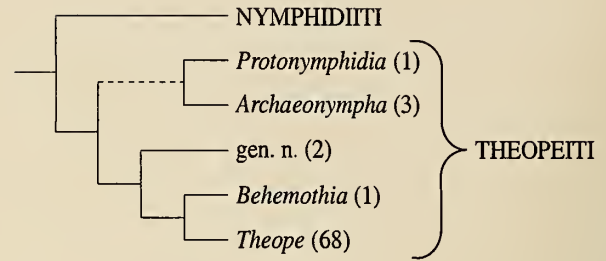


FIG. 1. A generic-level phylogeny for the nymphidiine riodinid subtribe Theopeiti (*sensu* Hall 1999a), the putative sister clade to the subtribe Nymphidiiti (*sensu* Hall 1999a), adapted from the species-level phylogeny of Hall (1999a). Numbers in parentheses represent the number of species in each genus. The dashed line indicates uncertainty regarding the sister group relationship of *Protonymphidia* and *Archaeonymphia*; *Protonymphidia* may form a distinct lineage at the very base of the Theopeiti.

(1997) all raised doubts as to the monophyly of *Pandemos*. In fact, each *Pandemos* species belongs in a different subtribe of the Nymphidiini (*sensu* Hall 1999a). Harvey (1987), and subsequently DeVries (1997), noted that *palaeste* actually belonged in the genus *Synargis* Hübner, [1819] (subtribe Lemoniaditi (*sensu* Hall 1999a) = Lemoniini Auctt—see Hall & Heppner 1999, Hall 1999a, b), after the early stages and genitalic structures had been examined. Harvey (1987) was also the first to note that *godmanii* was not closely related to *pasiphae*, but its true systematic affinities have remained unknown. However, recent cladistic studies of the tribe Nymphidiini indicate that by virtue of possessing a ventrally positioned spiracle on male abdominal segment three (the character proposed by Harvey (1987) as a synapomorphy for his Nymphidiini) and lacking sclerotized tissue joining the male genitalic valve tips, *godmanii* belongs in the subtribe Theopeiti (Hall 1999a, b). A morphological cladistic analysis of the subtribe Theopeiti (see introduction) indicates that *godmanii* represents the sister clade to the large genus *Theope* (Hall 1999a, b) (see Fig. 1), although the only universal synapomorphy that unites these two clades is the resting posture of their members; all species rest with their wings closed over the body instead of outspread (DeVries 1997, Hall 1999a, b), as is typical for the Riodinidae. However, *godmanii* lacks the wing pattern and male abdominal synapomorphies that support the monophyly of the recently revised genus *Theope* (Hall 1999b). The large morphological differences separating *godmanii* from its nearest relatives necessitate the description of a new genus for it. *Pandemos* should be regarded as a monotypic genus of the subtribe Nymphidiiti (*sensu* Hall 1999a).



FIGS. 2-3. 2. *Behemothia godmanii* (Dewitz, 1877), Mexican male: A, dorsal surface; B, ventral surface. Mexican female: C, dorsal surface; D, ventral surface. 3. *Protonymphidia senta* (Hewitson, 1853), Brazilian male: A, dorsal surface; B, ventral surface. Brazilian female: C, dorsal surface; D, ventral surface.

Biology: Very little is known about the biology of the single *Behemothia* species, *godmanii*. Museum label data indicate that this uncommon species occurs primarily in relatively dry semi-deciduous woodlands, and de la Maza and de la Maza (1993) report it as occurring from 100 to 700 m in Chiapas, Mexico. DeVries (1997) reports finding a female in Belize perched beneath a branch with its wings folded over the body and the forewings dropped back into the hindwings. The foodplants and early stages remain undiscovered, but the position of *Behemothia godmanii* in the Nymphidiini indicates that the larvae will be myrmecophilous (Harvey 1987).

Distribution: *Behemothia godmanii* is known to range from central Mexico to Costa Rica.

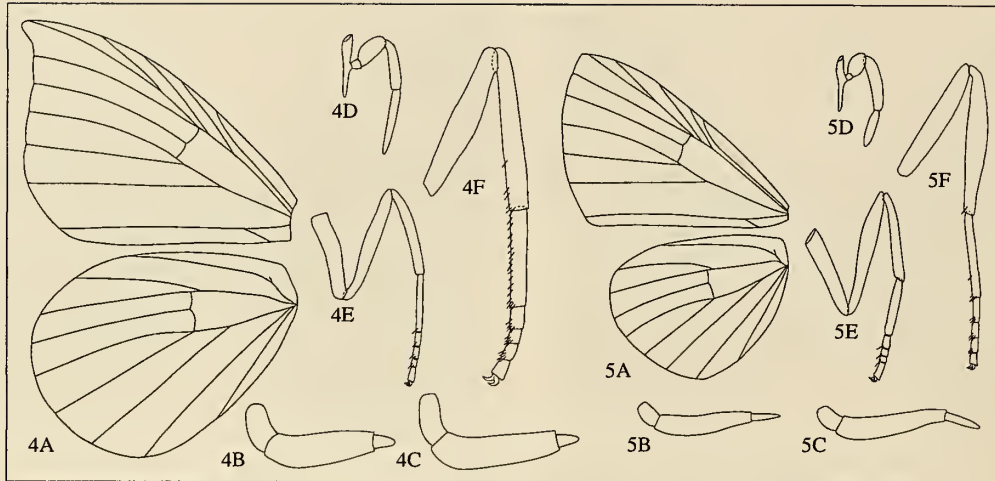
Protonymphidia Hall, new genus

Figs. 3A-D; 5A-F; 7A-D

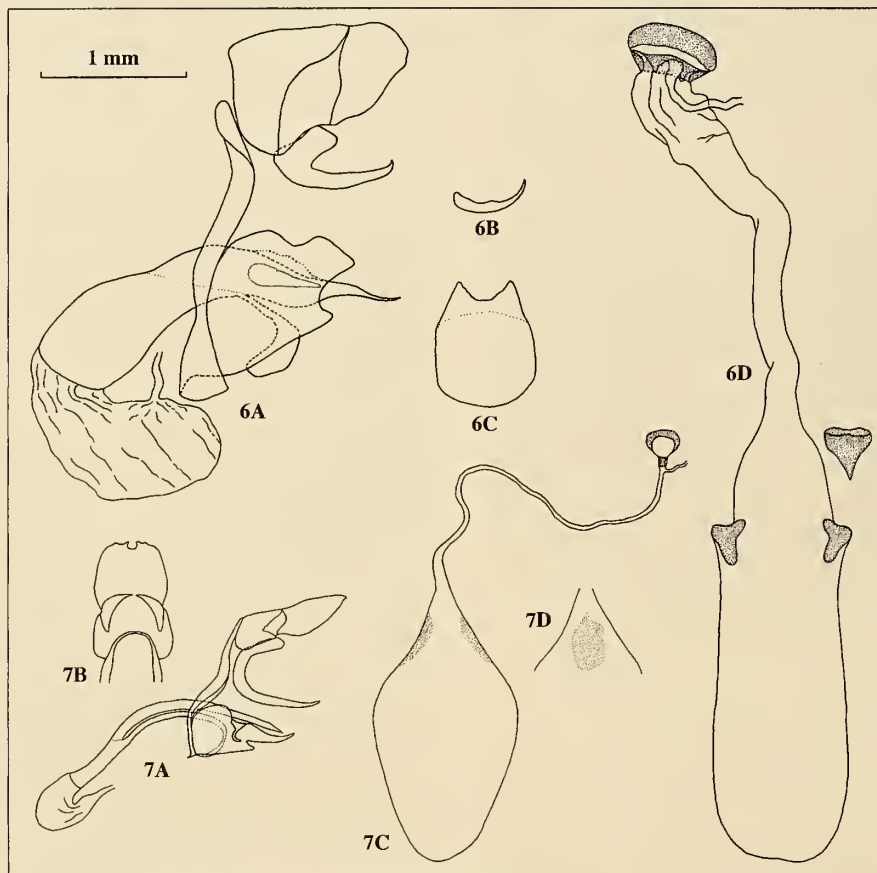
Type species. *Protonymphidia senta* (Hewitson 1853).

Description. MALE: typical forewing length 14.5–15.5 mm. *Wing shape:* both wings somewhat elongate; forewing costa straight, distal margin relatively straight; hindwing elliptical, rounded at tornus and apex. *Venation* (Fig. 5A): four forewing radial veins. *Dorsal surface:* forewing ground color dark orange; paler orange at very wing base, one dark brown spot at base of discal cell ringed by pale orange, another at middle of cell, a similar elongate line marking cell end with an additional line of paler orange proximally, two similar spots towards base of cell Cu2 below those in dis-

cal cell; a pale orange postdiscal band kinks proximally at vein M3, a disjointed line of postmedial dark brown lines surrounded by paler orange extends from costa to vein 2A, small patch of white scaling distal to mark in cell R4+5; a column of dark brown spots at submargin faintly ringed by slightly paler orange extends from cell Cu2 to cell R3, two spots in former and one in remainder, few white scales at proximal edge of apical spots; distal fringe dark orange. Hindwing similar to forewing except anal margin cream, two prominent white marks present in cell R4+5 at costa, one postdiscal and one discal, and basal brown spots less prominent with additional one towards base of cell R4+5; white scaling present at middle of distal margin of cells Cu2 to R4+5. *Ventral surface:* forewing ground color orange-brown; pattern elements same as on dorsal surface except paler orange areas very pale orange-cream and more extensive, five additional evenly spaced small dark brown spots present along costa, and veins outlined in pale orange-brown. Hindwing ground color orange-brown; pattern elements same as on dorsal surface except paler orange areas very pale orange-cream and more extensive, two additional dark brown spots visible at base of costa, and veins outlined in pale orange-brown. *Head:* ventral surface of labial palpi cream, distal third of elongate second segment and entire elongate third segment brown dorsally, remainder orange (Fig. 5B). Eyes bare and brown (in dried specimens), dark orange scaling at margins. Frons dark orange. Antennae brown with whitish scaling at base of each segment ventrally, narrow nudum region devoid of scaling along inner edge of shaft; tubular clubs brown, tips orange-brown. *Body:* dorsal surface of thorax and abdomen, including patagia, dark orange, ventral surface pale orange-cream. Forelegs pale orange-cream, femurs of mid and hindlegs pale orange, remainder dark orange; tarsus of foreleg unimerous and short, coxa elongate (Fig. 5D); midleg and hindleg with a tibial spur and a group of spines at inner distal tip of tarsal segments one to four, tibia broader at middle (Fig. 5F). *Genitalia* (Figs. 7A, B): uncus very elongate, especially dorsally, with rounded notch and two small points at middle of distal dorsal edge, separated from rec-



FIGS. 4-5. Morphology. 4. *Behemothia godmanii* (Dewitz, 1877): A, male venation; B, male palpus; C, female palpus; D, male foreleg; E, female foreleg; F, male hindleg. 5. *Protonymphidia senta* (Hewitson, 1853): A, male venation; B, male palpus; C, female palpus; D, male foreleg; E, female foreleg; F, male hindleg.



FIGS. 6-7. Genitalia (setae of male genitalic unci and valvae are omitted for clarity). 6. *Behemothia godmanii* (Dewitz, 1877): A, male genitalia in lateral view; B, dorsal view of aedeagal cornutus; C, ventral view of last (eighth) abdominal sternite; D, female genitalia in dorsal view with lateral view of signa. 7. *Protonymphidia senta* (Hewitson, 1853): A, male genitalia in lateral view; B, dorsal view of uncus; C, female genitalia in dorsal view; D, lateral view of corpus bursa.

tangular tegumen by rectangular lateral fenestration; falci very elongate; vinculum broader at middle, forms tiny saccus ventrally, narrows considerably around anterior margin of tegumen; valvae consist of large basal bulge with downwardly pointed remainder divided by weakly sclerotized tissue dorsally, triangular point at middle of ventral margin; aedeagus long and very narrow with triangular tip; pedicel very elongate, evenly narrow and rounded. Last tergite and sternite plain rectangles, middle of distal margin of last sternite weakly sclerotized.

FEMALE: differs from male in following ways: both wings with more convex distal margins. *Dorsal surface:* paler orange areas broader, white scaling proximal to submarginal brown spots more extensive and present around entire submargin, white scaling in forewing cell R4+5 and at hindwing costa more prominent and also present distal to tiny dark brown marks in forewing cells R3 and R2, and at base and middle of hindwing cell R4+5. *Ventral surface:* ground color slightly paler, especially distally, pale orange-cream areas more extensive. *Head:* second palpal segment slightly more elongate, third segment markedly more elongate (Fig. 5C). Nudum region along inner edge of shaft considerably broader. *Body:* foreleg with single long spine at inner distal tip of tarsal segments two to four (Fig. 5E). *Genitalia* (Figs. 7C, D): corpus bursae round, signae consist of a small ovoid sclerotized band either side of ductus bursae opening; ductus bursae and ductus seminalis unsclerotized and very narrow; ostium bursae small with broad sclerotized band dorsally and only soft tissue ventrally.

Diagnosis. The single species of *Protonymphidia*, *P. senta*, presents a unique phenotype in the Riordinidae. The slightly elongate wing shape, entirely pale and dark orange dorsal surface and orange-brown and cream banded ventral surface are quite distinctive. The ventral patterning closely resembles that of *Archaeonympha* species, but they all have black and blue dorsal surfaces and distinct morphology (see below).

Etymology. The name is derived from the Greek words for "first" or "primitive", and "nymph", in reference to the basal position of the genus in the subtribe Theopeiti.

Systematic position: The taxon *senta* was described by Hewitson (1853) in the genus *Lemonias* Hübner, 1807, then subsequently transferred to *Echenais* Hübner, [1819], by Kirby (1871), and *Adelotypa* by Bridges (1988, 1994) for nomenclatural reasons (see Hemming 1967). However, cladistic studies involving the tribe Nymphidiini indicate that *Adelotypa* is a polyphyletic genus, and the taxon *senta* is not closely related to the type species of *Adelotypa*, *bolena* Butler, 1876 (Hall & Harvey 1998, Hall 1999a, unpubl. data). In fact, whilst *bolena* is a relatively derived member of the subtribe Nymphidiiti (Hall unpubl. data), *senta* is a plesiomorphic member of the subtribe Theopeiti, and a comprehensive morphological cladistic analysis of that subtribe (see introduction) indicates that *senta* is most closely related to the genus *Archaeonympha* (see Fig. 1) (Hall & Harvey 1998, Hall 1999a). Characters that place *senta* at the base of the Theopeiti include the plain rectangular shape of the last male abdominal sternite and the complete (albeit very narrow) vinculum dorsally, which is complete in the majority of members of the subtribes Lemoniadiiti and Nymphidiiti, and incomplete (totally absent dorsally) in the remaining species of the Theopeiti. The fact that *senta* lacks the synapomorphies of *Ar-*

chaeonympha, especially the unique synapomorphy of the ductus bursae of the female genitalia (see Hall & Harvey 1998), and every other genus in the Theopeiti, and possesses an unusually high number of autapomorphies, such as the sclerotized signal bands on the corpus bursae of the female genitalia and the very elongate falci and dorsally notched uncus of the male genitalia, amply justify the description of a new genus for it.

Biology: The single species of *Protonymphidia*, *senta*, is locally common along forest edges, stream-sides, and in secondary growth habitats, where it is typically encountered in association with its foodplant *Bauhinia* (Leguminosae). Several individuals of both sexes may be found feeding simultaneously from the extrafloral nectaries of this plant where they remain unmolested by the resident ants, identified by DeVries et al. (1994) as *Pheidole* nr. *biconstricta* (Myrmicinae). Oviposition appears to be dependent on the presence of these ants, and the larvae are tended by them. The myrmecophilous larvae, which are yellow-brown to pale green, covered with tiny granulations, and possess a fringe of ventro-lateral setae that are especially long on the first thoracic segment, feed on leaf tissue between the main veins and also on the extrafloral nectaries; the pupa is brown with a slight dorsal keel (DeVries 1997, J. Turner pers. comm.).

Distribution: *Protonymphidia senta* occurs throughout the western Amazon basin from Colombia to Bolivia and in the western half of Amazonian Brazil.

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